MORPHOLOGICAL AND ECOLOGICAL SEGREGATION OF TWO SYMPATRIC *LOMATIUM TRITERNATUM* (APIACEAE) VARIETIES IN MONTANA

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ABSTRACT

The *Lomatium triternatum* complex is widespread in the Columbia River Basin. *Lomatium triternatum* (Pursh) J. M. Coult. & Rose var. *triternatum* and *L. triternatum* (Pursh) J. M. Coult. & Rose var. *anomalum* (M. E. Jones ex J. M. Coult. & Rose) Mathias are sympatric throughout much of their range and are reported to have similar fruit but different leaves. Plants of the two varieties repeatedly occur within 5–30 m of each other at an unusual site in northwest Montana, USA. We collected data on leaf and fruit morphological characters and habitat associations at this site to help address whether the proper taxonomic rank for these two taxa should be revised. Terminal leaflet shape and specific leaf area differed between the two varieties with little or no overlap. Fruit mericarp length and width also differed between the two varieties. These patterns are not consistent with treating *L. triternatum* var. *triternatum* and *L. triternatum* var. *anomalum* as sympatric, interbreeding, conspecific taxa. The two varieties of *L. triternatum* also occurred in different plant communities in spite of growing in close proximity: var. *anomalum* occurs with tall, leafy forbs, while var. *triternatum* is associated with xeric-adapted bunchgrasses and cushion-forming forbs. We conclude that the two varieties are better recognized as separate species.

Key Words: Apiaceae, Columbia Basin, *Lomatium triternatum*, Montana.

Lomatium is the largest North American genus in the Apiaceae with its main center of diversity in the Columbia Plateau and Intermountain West (Mathias 1938; Sun and Downie 2010). Analysis of molecular data suggests that *Lomatium* and other closely allied genera probably underwent rapid diversification during the late Tertiary (Sun et al. 2004). As a result, the genus is taxonomically difficult (Mathias 1938), with relatively few taxonomically informative morphological traits, numerous narrow endemic species (Darrach et al. 2010), and a good deal of morphological convergence (Sun and Downie 2010).

The *Lomatium triternatum* (Pursh) J. M. Coult. & Rose complex is widespread in the Columbia River Basin. The complex has been variously treated as seven species (Coulter and Rose 1900), two species consisting of seven varieties (Mathias 1938), and one species consisting of three varieties (Hitchcock et al. 1961; Cronquist et al. 1997). The complex is loosely united by the following characters: narrow involucel bracts, similar mericarp shape, and vaguely similar leaf shape. Hitchcock and Cronquist (1973), in the most recent treatment for the Pacific Northwest, use a tripartite classification with two subspecies: *L. t.* subsp. *triternatum* and *L. t.* subsp. *platycarpum* (Torr.) B. Boivin (= *L. simplex* [Nutt. ex S. Watson] J. F. Macbr.). Subspecies *triternatum* is composed of two varieties: var. *triternatum* and var. *anomalum* (M. E. Jones ex J. M. Coult. &

Rose) Mathias. Here we explore the taxonomic disposition of these two varieties. They are reported to have similar fruit but distinctly different leaves. Variety *triternatum* has bipinnate or biternate leaves with linear leaflets, while var. *anomalum* has bipinnate to tripinnate leaves with narrowly oblong leaflets. These two varieties are reported to be "wholly intergradient" (Cronquist et al. 1997), but no further information is provided. Variety *triternatum* occurs from southern Alberta and British Columbia to northern California and northern Utah, while var. *anomalum* is found sporadically from northwest Montana to eastern Washington south to southwest Oregon, across much of Idaho to northern Utah and southwest Wyoming (Cronquist et al. 1997; Consortium of Northwest Herbaria 2011).

Possession of similar morphological traits can often indicate a close phylogenetic relationship between species. Indeed, similar morphology, especially in the anatomy of reproductive structures, has long formed the basis of classical systematics (Stace 1980). However, similar morphology may actually be the result of convergent evolution rather than an indication of close phylogenetic relationship (Niklas 1997; Judd et al. 2008). Indeed, recent molecular studies show that convergent evolution has occurred in the Apiaceae, and fruit morphology in particular is reported to be a poor indicator of phylogenetic relatedness in the family (Downie et al. 2002).

Under the biological species concept, two species will rarely if ever interbreed to produce fertile offspring, but interbreeding is possible and likely in a zone of overlap between two subspecies or varieties of the same species (Mayr 1942; Stace 1980). Both *L.* var. *triternatum* and *L. t.* var. *anomalum* occur together in an unusual geologic setting in northwest Montana known as the Giant Ripple Marks. Plants of the two varieties repeatedly occur within 5–30 m of each other. The purpose of our study is to determine the degree to which these two taxa may intergrade ecologically and/or morphologically at this site in order to inform an independent assessment of their proper taxonomic rank.

STUDY SITE

We conducted our study in the Giant Ripple Marks at the north end of Camas Prairie Basin at an elevation of ca. 885 m, 8 km south of the town of Hot Springs on the Flathead Indian Reservation in Sanders Co., Montana (47°30.9′N, 114°35.0′W). The climate of this region is semi-arid with cold winters and hot summers. The most similar weather recording station to the study site is at Lonepine, 15 km to the north. The mean January and July temperatures are −5.2°C and 20.1°C, respectively. The average annual precipitation is 286 mm (NCDC 2012). The majority of the precipitation occurs from April through June.

The Giant Ripple Marks were formed when Glacial Lake Missoula drained during Pleistocene glacial retreats, and water poured south over passes at the north end of the Camas Prairie Valley. The water dumped its load of coarse sediments in two lines of enormous current ripples (Alt and Hyndman 1986). These ripple marks appear today as two series of low (5–20 m), parallel ridges roughly perpendicular to the main axis of the valley (Fig. 1). The vegetation of the Giant Ripple Marks is a mosaic of bunchgrass prairie on the well-drained ridges with graminoid and forb-dominated meadow vegetation and occasional vernal pools on the deeper, fine textured soils in the swales between the ridges. The tops and upper and middle slopes of the ripple mark ridges are dominated by the grasses *Pseudoroegneria spicata* (Pursh) Á. Löve, *Poa secunda* J. Presl, and *Elymus elymoides* (Raf.) Swezey and the cushion-forming forbs *Eriogonum ovalifolium* Nutt. and *Antennaria dimorpha* (Nutt.) Torr. & A. Gray. *Bromus tectorum* L. is an annual, exotic grass that is common particularly where the perennial grasses have declined due to grazing. Vegetation of the swales is currently dominated by introduced species such as *Poa pratensis* L. and *Potentilla recta* L. The most common native species in the swales include the grasses *Elymus elymoides* and *Poa secunda*

and the forbs *Lomatium triternatum* var. *anomalum*, *Artemisia ludoviciana* Nutt., and *Lupinus sericeus* Pursh.

METHODS

We located a 50-m transect across six haphazardly chosen ripple marks in early June 2009 so that approximately half of each transect was on the slope of the ridge, and the other half was in the swale at the bottom. We sampled the closest *Lomatium triternatum* plant to the transect line at 5-m intervals, providing 10 samples per transect and a total of 60 target plants. We classified each plant into either var. *triternatum* (narrow leaflet) or var. *anomalum* (broad leaflet) and measured the length and maximum width of the terminal leaflet of the lowest leaf for each plant in the field and then immediately placed the leaflet in a plant press. Senescent or damaged leaves were avoided. We dried collected leaves for 24 hr and weighed each one to the nearest mg.

Vegetation associated with each target plant was quantified by placing a 1-m² plot frame with the target plant in the center and estimating canopy cover of each vascular plant species into one of the following classes: 0.1%, 1%, 5%, 10%, 15%, etc. Native plot vegetation was ordinated using principal components analysis (PCA). Only species occurring in at least five plots were included in the analysis. Non-native species, such as *Agropyron cristatum* (L.) Gaertn. *Bromus tectorum*, and *Potentilla recta*, were common in some plots but were excluded from the analysis. Nomenclature follows Lesica (2012).

We collected mature fruits (mericarps) from haphazardly chosen plants of both *L. triternatum* taxa on June 18, June 24, and July 10, 2008. Length and width of randomly chosen mericarps
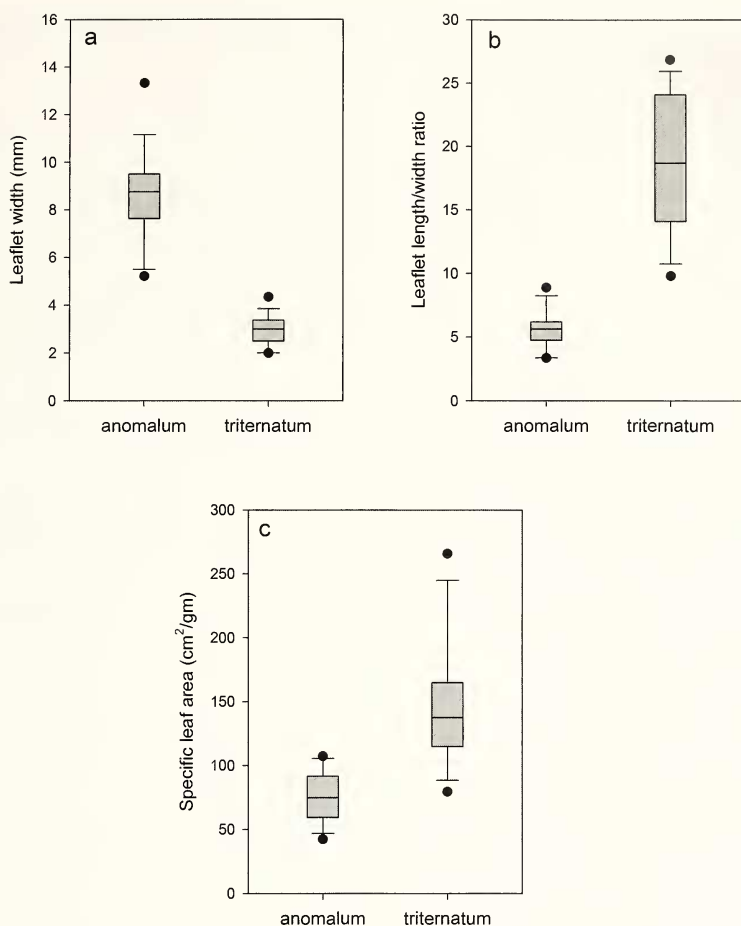
Fig. 2.   Width (a), length/width ratio (shape) (b), and specific leaf area (c) for terminal leaflets of *Lomatium triternatum* var. *anomalum* and var. *triternatum*. The box represents the middle 50% of the scores with the vertical line the median; the upper and lower whiskers mark the range of values excluding outliers; the dots represent the 5th and 95th percentiles.

and their enclosed seed were measured to the nearest 0.1 mm with a dissecting microscope. Within-morphotype measurements did not differ among dates (P ≥ 0.15), so we combined measurements from different dates in our analyses to provide a sample of n = 40 for each taxon.

Leaf area (cm²) was measured on the dried leaf collections with a LI-COR 3100 area meter (LI-COR, Lincoln, NE). Surface area of each leaflet was measured three times and averaged. Specific leaf area (SLA) for each target plant was calculated as the ratio of the average of the three surface area measurements to leaf dry mass (cm²/g). We used two-sample t-tests to assess the difference in leaflet shape, specific leaf area, and fruit size and shape.

RESULTS

Shape of the terminal leaflets differed between the two varieties with little overlap. Leaflet length

did not differ between the two varieties (P = 0.11). However, leaflet width was significantly greater for *L. t.* var. *anomalum* compared to var. *triternatum* (P < 0.001; Fig. 2a), and length/width ratio for the terminal leaflet of var. *triternatum* was greater than 10 but less than 10 for var. *anomalum* (P < 0.001; Fig. 2b). Specific leaf area (SLA) also differed between varieties. Mean SLA was 148 cm²/g (SE = 9) and 76 cm²/g (±4) for var. *triternatum* and var. *anomalum*, respectively (t = 7.0, P < 0.001), and there was little overlap between the two varieties (Fig. 2c).

Some fruit characters also differed between the two varieties. Mean mericarp length was 7.0 mm (SE = 0.1) and 8.6 mm (±0.2) for var. *triternatum* and var. *anomalum*, respectively (t = 7.9, P < 0.001), and width was 4.2 mm (±0.1) and 4.8 mm (±0.1), respectively (t = 5.1, P < 0.001). However, fruit shape (length-width ratio) did not differ between the two varieties (P = 0.30). The ratio of the width of one side of the
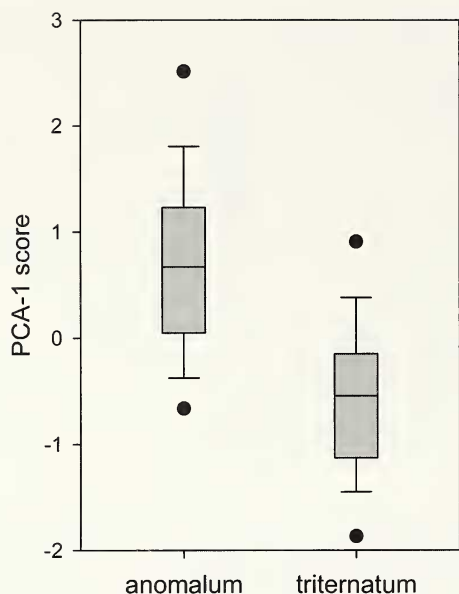
FIG. 3. First principal component analysis (PCA) scores for vegetation associated with *Lomatium triternatum* var. *anomalum* and var. *triternatum*. The box represents the middle 50% of the scores with the vertical line the median; the upper and lower whiskers mark the range of values excluding. The dots represent the 5th and 95th percentiles. Higher PCA scores were associated with more mesic vegetation.

mericap wing to the width of the enclosed seed was 0.56 (±0.02) and 0.49 (±0.03) for vars. *triternatum* and var. *anomalum*, respectively (t = 2.2, P = 0.028).

The two varieties of *Lomatium triternatum* occurred in different plant communities. The first axis of the PCA accounted for 17% of the total variation in the associated vegetation data. PCA 1 represented a gradient between xeric vegetation dominated by the grass *Pseudoroegneria spicata* and the cushion-forming forbs *Antennaria dimorpha* and *Eriogonum ovalifolium,* and a more mesic assemblage dominated by taller, leafier forbs including *Achillea millefolium* L., *Lupinus sericeus*, *Lomatium macrocarpum* (Torr. & A. Gray) J. M. Coult. & Rose, and *L. triternatum* var. *anomalum*. Twenty-seven plants of var. *triternatum* (84%) had a PCA-1 score <0, while 22 of var. *anomalum* plants (79%) had a score >0 (Fig. 3). Other axes were not interpretable.

DISCUSSION

The two *Lomatium* taxa discussed here were associated with different habitats at our study site. Plants assigned to var. *anomalum* were found only in swales dominated by tall, leafy forbs, while var. *triternatum* was common in more xeric, ridgetop and slope communities dominated by relatively sparse *Pseudoroegneria spicata* tussocks

and cushion-forming forbs. Different communities often host different congeners (Schluter 2000).

By definition infraspecific taxa should be interfertile to some extent where they co-occur (Stace 1980), so we would expect to find plants of intermediate morphology when two varieties of the same species are closely sympatric, as in our study area. However, these two putative varieties of *Lomatium triternatum* remain morphologically distinct in spite of occurring in close proximity. Mericarps of var. *anomalum* are larger than those of var. *triternatum* with little overlap, and leaflets of var. *anomalum* are wider than those of var. *triternatum* with no overlap. The two taxa differ in both fruit and leaf traits, which are unrelated characters likely coded for by different genetic pathways. For example, phenotypic differences in fruit and leaf traits have been shown to be attributed to different molecular traits or developmental pathways (Lippman and Tanksley 2001; Thul et al. 2009). Since traits among these two *Lomatium* taxa appear to be nearly discontinuous it suggests that they are genetically isolated in spite of occurring sympatrically.

Specific leaf area (SLA) for var. *triternatum* was nearly twice as great as for var. *anomalum*. Both infraspecific and interspecific differences in specific leaf area (SLA) have been linked to water stress (Fitter and Hay 2002; Hoffmann et al. 2005). Plants occurring in drought-prone areas tend to have lower SLA (thicker leaves) than those in more mesic environments (Reich et al. 1997; Cunningham et al. 1999; Wright et al. 2001; Hoffmann et al. 2005). Furthermore, plant species often express phenotypic plasticity in SLA—e.g., sun leaves have a lower SLA than shade leaves (Chazdon and Kaufmann 1993; Lichtenthaler et al. 2007). Thus, if the two forms of *Lomatium* were ecotypes of the same species, we would expect the swale var. *anomalum* to have a higher SLA than var. *triternatum,* which occurs in more xeric habitats. Instead, we found the opposite. Given the difference in SLA, it is unlikely that these forms are interbreeding and that morphological differences are simply a result of plasticity. In the case of these two taxa, the differences in SLA are more likely attributed to entirely different gene pools (White and Montes-R 2005), with SLA being a genetically determined morphological difference related to other traits such as water use (Nobel 1980), leaf temperature (Van Volkenberg and Davis 1977), or internal anatomical differences (Nobel 1991). SLA may not evolve independently of other morphological traits; var. *anomalum* may belong to a lineage with relatively low SLA that has been conserved along with other adaptations, such as large leaves, which correspond to its relatively mesic habitat. Our combined morphological results suggest that the two taxa are not exchanging

genes for SLA or other leaf and fruit traits and may not even belong to the same lineage within *Lomatium*. Indeed, recent molecular-based phylogenetic research indicates that the two taxa belong to separate clades (D. Mansfield, College of Idaho, personal communication).

Lomatium triternatum var. *anomalum* and *L. t.* var. *triternatum* occupy different habitats in northwest Montana and have different leaf and fruit morphologies with little or no overlap even when populations occur intermixed. In addition, differences in leaf anatomy between the two taxa are likely genetically determined. Taken together, our results from this site of sympatry support treatment of *Lomatium triternatum* var. *anomalum* as a separate species: *Lomatium anomalum* M. E. Jones ex J. M. Coult. & Rose.

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